A STOCK ASSESSMENT MODEL OF ANTARCTIC TOOTHFISH (*DISSOSTICHUS MAWSONI*) IN THE ROSS SEA REGION INCORPORATING MULTI-YEAR MARK-RECAPTURE DATA

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Abstract

An exploratory longline fishery for Antarctic toothfish (*Dissostichus mawsoni*) has been carried out in the Ross Sea region since the late 1990s. No fishery-independent methods of monitoring stock abundance were plausible, and hence a multi-year mark-recapture tagging program was initiated by New Zealand fishing vessels in 2001, and tagging has been an ongoing requirement for all vessels fishing in the fishery since 2004. Although tagging experiments are commonly used for assessing fish stocks, most rely on estimates of abundance from a single release and subsequent recapture events. An integrated Bayesian stock assessment model was developed for Antarctic toothfish in the Ross Sea region that incorporates multi-year release of tagged fish and subsequent multi-year data of recapture of tagged fish in conjunction with fishery catch-at-age data.

This is the first published stock assessment of toothfish in the Ross Sea region. It demonstrates the value of multi-year mark-recapture programs to estimate fish stocks even where no fishery-independent estimates of adult biomass are available.

Monte-Carlo Markov Chain (MCMC) estimates of initial (equilibrium) spawning stock abundance (B_0) were 68 790 tonnes (95% credible intervals 59 540–78 470), and current (B_{2013}) biomass was estimated as 74.8% B_0 (95% CIs 71–78). Sensitivity analyses carried out showed the data selection provided a precautionary estimate of biomass, and that these estimates were insensitive to selectivity assumptions regarding cryptic biomass of older fish. Results also suggested that a sub-adult survey series that started in 2012 will provide a useful signal indicative of recruitment fluctuations as the time series develops, a signal which is not present in the fishery-dependent data.

Introduction

Toothfish are large Nototheniids endemic to Antarctic and sub-Antarctic waters. There are two species of toothfish: Antarctic toothfish (*Dissostichus mawsoni*) and Patagonian toothfish (*D. eleginoides*). Their distribution is circumpolar, although *D. mawsoni* have a more southern distribution and are found in latitudes south of the Antarctic Convergence (Gon and Heemstra, 1990).

Finfish fisheries in Antarctic waters are largely managed under the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR). To date, the main fishery for Antarctic toothfish in the high seas of the CAMLR Convention Area has taken place in the Ross Sea region. For purposes of management, the 'Ross Sea region' (RSR) is defined to include the area between 150°E and 150°W. A distinct fishery also operates further east, in the 'Amundsen Sea region' (ASR), and is managed separately (Figure 1).

The RSR exploratory longline fishery was initiated in 1997[1] and now attracts 15–25 vessels from 6
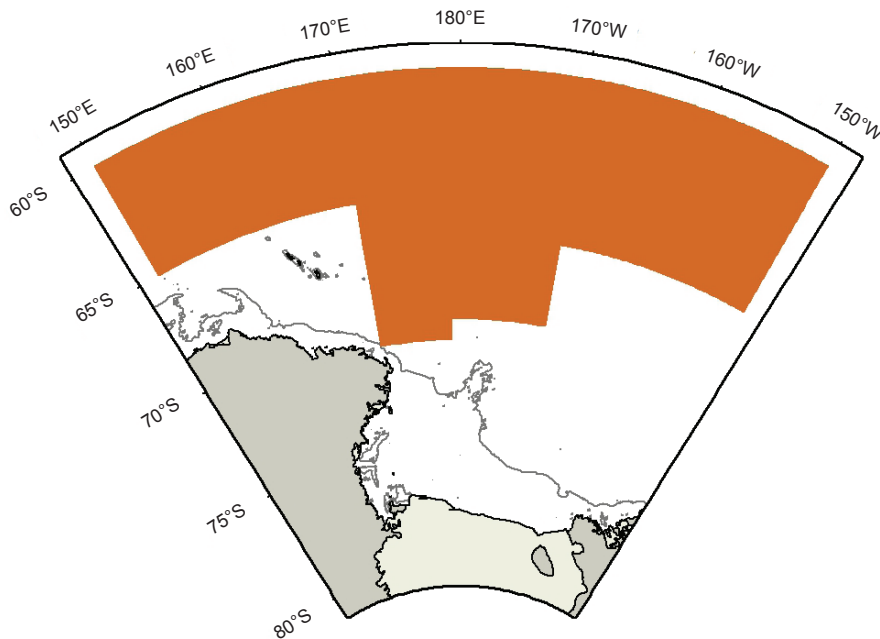
Figure 1: The Ross Sea region with 800 m depth contour and the three fisheries: shelf shallower than 800 m, slope deeper than 800 m and north in brown. Also shown is the Antarctic continent (dark grey), Ross Sea permanent ice shelf (light grey) and the 1 000 m depth contour.

to 10 nations each year (Hanchet et al., 2013). Initially, catch limits were derived by comparing longline catch rates between vessels in the RSR and vessels in other toothfish fisheries in the CCAMLR area (SC-CAMLR, 2002), but as catches increased, there was a need to develop a more reliable method for estimating abundance and yields for the stock.

The use of catch-at-age models in fish stock assessments has become common practice for stocks where a time series of catch and age composition is available. However, catch and age composition alone are rarely sufficient to reconstruct the history of a fish population, and statistical catch-at-age analyses require auxiliary information to accurately estimate changes in abundance (Deriso et al., 1985; Doubleday, 1976; Fournier and Archibald, 1982; McAllister and Ianelli, 1997; Methot, 1990). Survey-based relative or absolute abundances are commonly used to provide abundance information in catch-at-age analyses. In the absence of fishery-independent data, catch-effort statistics from fisheries have often been used. However, catch-per-unit-effort (CPUE) indices may be unreliable as indices of abundance (Harley et al., 2001), particularly in developing fisheries with short time series of effort.

Alternate methods to catch-at-age analysis for estimating fishing mortality rates and stock abundance include various forms of mark-recapture analysis (Pollock et al., 1991; Ricker, 1975; Seber, 1982). Integrated statistical catch-at-age models have used mark-recapture data in models to inform natural mortality and/or movement (e.g. Everson et al., 2009; Goethel et al., 2014; Hampton and Fournier, 2001; Punt et al., 2000) and occasionally abundance (Candy and Constable, 2008; Haist et al., 2005; Hillary and Agnew, 2006). Extended reviews of the different uses of mark-recapture data in stock assessments are detailed elsewhere (e.g. Goethel et al., 2011; Maunder and Punt, 2013). In this instance, natural mortality was assumed known (see Appendix A for details), movement was assumed contained within the stock and uniform in the RSR, and mark-recapture data were used as an index of absolute abundance of the fish population in the RSR.

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[1]   The CCAMLR fishing season starts on 1 December and ends on 30 November in the following year. In the Ross Sea, fishing extends from December to May and so in this paper the period 1 December 2008 to 30 November 2009 would be referred to as 2009.

For the Antarctic toothfish stocks in the RSR, time series of catch, CPUE and commercial catch age-composition data have been developed. However, no fishery-independent survey data were available and there were concerns that changes in CPUE data reflected increasing fisher knowledge and experience, variable ice cover and vessel interactions rather than indexing abundance (Candy and Constable, 2008; Hanchet et al., 2013; Parker et al., 2013a; Hillary and Agnew, 2006). A pilot mark-recapture program was initiated by New Zealand vessels in 2001 and after the subsequent recapture of several tagged fish, the program was expanded by CCAMLR to become a requirement of vessels fishing in the fishery (SC-CAMLR, 2004). It is a requirement for all vessels fishing in the Ross Sea toothfish fishery to tag toothfish at a rate of 1 fish per tonne landed, with the size composition of tagged fish that approximates that of the catch.

However, the problem with longer-term mark-recapture programs is that the fish undergo changes in growth rate and natural mortality as a result of being tagged, which needs to be accounted for explicitly within the estimation process. The objective of this paper is to report on the development of a population model which explicitly deals with multi-year mark-recapture data and allows the inclusion of parameters for tag-related growth retardation, tag-related mortality and tag loss. It shows that low-level multi-year mark-recapture programs can be used for stock assessment purposes, even where no fishery-independent surveys are available.

Fishery management in the RSR and in most of the Antarctic region is controlled by CCAMLR. As a result, most of the research described herein has been carried out to inform CCAMLR management and has been reported to, presented at and reviewed by, CCAMLR working groups, in particular the Working Group on Statistics, Assessments and Modelling (WG-SAM) and the Working Group on Fish Stock Assessment (WG-FSA). These working papers are available from the authors only on request. All reports from these working groups and CCAMLR decisions are available from the CCAMLR website as Scientific Committee reports (SC-CAMLR) or Commission reports. Whilst the authors have tried to keep the number of such references to a minimum, the nature of the research is such that this was not always possible. The aim of this paper is to collate existing information pertaining to the stock assessment for Antarctic toothfish in the Ross Sea region into a single publicly available source.

Framework

Stock structure

Antarctic toothfish have a circumpolar distribution extending north to the Antarctic Convergence (Gon and Heemstra, 1990). Analysis of genetic data has shown that fish within the Pacific sector of the Southern Ocean (including the RSR) are genetically differentiated from those in the Atlantic and Indian sectors (Kuhn and Gaffney, 2008). Within the Pacific sector, there is weak evidence for genetic separation of toothfish between the RSR and the ASR (Kuhn and Gaffney, 2008).

Data of toothfish tagged and subsequently recaptured has so far shown very limited movement of fish between the RSR and the ASR (Parker et al., 2013a): a single tagged toothfish released at McMurdo Sound has been recaptured in the ASR, one fish tagged by the fishery having moved from the RSR to the ASR, and two from the ASR to the RSR. Furthermore, the hypothetical life history of Antarctic toothfish in the RSR (Hanchet et al., 2008) and its known circulation and hydrography (Rickard et al., 2010) suggest that for management purposes the RSR fishery, including SSRUs 882A and B (190°W to 210°W), should be treated separately from the ASR.

For stock assessment purposes, the RSR stock was further split into three fisheries reflecting three distinct age frequencies of the population, and spatial differences in associated catches in different years. This was based on work by Hanchet et al. (2008), who hypothesised an ontogenetic movement of toothfish: following recruitment of sub-adults to the continental shelf of the RSR, adults move to waters deeper than 800 m on the slope and then north to seamounts as spawners (Figure 1). This is reflected in the age frequency and gonad maturity stages of toothfish caught in the fishery (Hanchet et al., 2013; Parker et al., 2013a). Further details on the exact split between the shelf, slope and north fisheries of the RSR are given in Hanchet et al. (2013; Parker et al., 2013a).

The three fisheries and their specific selectivities represent the spatial heterogeneity of the

Table 1:   Biological parameters assumed for the modelling.

Relationship	Parameter	Value		
			Male	Female
Natural mortality	M (y^{-1})		0.13	0.13
von Bertalanffy	t_0 (y)		−0.256	0.021
	k (y^{-1})		0.093	0.090
	L_∞ (cm)		169.07	180.20
	CV		0.102	0.102
Length–weight	a		1.387e-08	7.153e-09
	b		2.965	3.108
	CV		0.1	0.1
Maturity	A_{50} ($\pm A_{to95}$)		11.99 ($\pm$ 5.25)	16.92 ($\pm$ 7.68)
Stock recruitment steepness (Beverton-Holt)	h	0.75		
Recruitment variability	σ_R	0.6		
Ageing error (CV)	CV	0.1		
Initial tagging mortality		10%		
Initial tag loss (per tag)		3.3%		
Instantaneous tag-loss rate (per tag)		0.062y^{-1}		
Tag-detection rate		98.8%		
Tag-related growth retardation		0.5 y		

population in the model as an alternative to modelling the three areas specifically with movement between the areas. However, modelling the RSR as a single area assumes full mixing of tags within the area, which is unlikely, and therefore a bias in the population estimate is likely. However, a fully spatially explicit operating model was built in order to estimate the extent of this bias (Mormede et al., 2014).

Model structure

The stock model was developed as a Bayesian sex- and age-structured population model of Antarctic toothfish in the RSR. The general structure and fitting procedures are detailed in Appendix B, whilst the choice of parameters is detailed in Appendix A. The values of the biological parameters used in the model are summarised in Table 1.

Observations

Data quality

In 2013, there were no fishery-independent data suitable for inclusion in the stock assessment of Antarctic toothfish from the RSR. For example, there were no fishery-independent surveys of the fished stock, as opposed to other parts of the Antarctic where trawl surveys have been carried out (Candy and Constable, 2008). However, a sub-adult

survey has been carried out since 2012 with the aim of developing an index of relative abundance of sub-adults in the southern Ross Sea and providing information on recruitment variability and autocorrelation (Parker et al., 2013b, 2013c). The recruitment index is currently too short to be included in the assessment but will be investigated for inclusion in future assessments as the time series develops.

Very few stock assessments rely solely on commercial data or commercial mark-recapture data (Haist et al., 2005; Hillary and Agnew, 2006). Because mark-recapture data are used to estimate abundance in the stock assessment and are collected from commercial vessels, the quality of these data is paramount.

Data from the RSR of fish recaptured with a tag suggested that tag-recovery rates varied between vessels more than expected by chance alone, and there was concern that the inclusion of unreliable tagging data may introduce bias into the assessment model. However, further analyses proved inconclusive, as potential vessel tagging performance was confounded with other factors such as the timing, location and size of fish tagged, as well as the location of the fishing effort in successive years. A relative index of vessel-specific tag detection performance for the Ross Sea fishery using a case-control methodology was developed (Mormede and Dunn, 2013). The method controls

Table 2:   Ross Sea Antarctic toothfish catch (tonnes) by fishery for 1997–2013.

Season	Fishery			Total	Catch limit[1]
	Shelf	Slope	North		
1997	0	0	0	0	1 980
1998	8	29	4	41	1 573
1999	14	282	0	296	2 281
2000	64	688	0	752	2 340
2001	113	347	133	593	2 314
2002	10	933	412	1 355	2 758
2003	2	609	1 158	1 769	4 135
2004	141	1 667	370	2 178	3 625
2005	397	2 262	550	3 209	3 625
2006	251	2 373	343	2 967	2 964
2007	68	2 438	573	3 079	3 072
2008	61	1 939	251	2 251	2 700
2009	135	1 904	393	2 432	2 700
2010	328	2 171	370	2 869	2 850
2011	483	2 054	347	2 884	2 850
2012	277	2 375	547	3 199	3 282
2013	260	2 450	411	3 121	3 282
Total	2 612	24 521	5 862	32 995	

[1]   Catch limit for the RSR and ASR combined for *Dissostichus* spp. for the years 1997–2005 and for the RSR for 2006–2009.

for the interannual spatial and temporal variability of commercial fishing operations from which tagged fish are released and recaptured. Selection criteria to determine a subset of vessels for which there was confidence in their tag-recapture data were developed and then applied, resulting in the mark-recapture dataset used for the assessment model. The selected 'quality' mark-recapture data included 72% of all released tagged fish and 80% of all recapture events of tagged fish in the RSR to 2013 whereby the release and subsequent recapture of tagged fish from vessels with lower than expected tag-recapture rates were excluded from the model. As a result, the use of the 'selected' trips dataset results in a lower (more precautionary) yield and is believed to have alleviated many of the problems associated with the previous 'all vessels' dataset.

Catch

The annual catch for Antarctic toothfish in the RSR, by fishery, as well as the catch limit in each year, is given in Table 2. Annual catch data were used as a direct input in the model.

Length- and age-frequency data

Length- and age-frequency data of toothfish in the RSR were described in detail by Hanchet et al. (2013) and Parker et al., 2013a. CCAMLR requires that all vessels fishing for toothfish in the Convention Area measure 35 toothfish per set. As a result, between 7 000 and 56 000 toothfish have been sexed and measured in the RSR each year since 1999. The length frequencies of Antarctic toothfish in each set were then multiplied by the catch in that set prior to being aggregated for each year and fishery to provide scaled length frequencies in each year and fishery.

Between 700 and 1 000 Antarctic toothfish from the RSR have been aged each year since 1998, assuming that one translucent zone is formed annually in the otoliths of this species. This ageing protocol was validated following the release and subsequent recapture of Antarctic toothfish tagged and injected with oxytetracycline (Horn, 2002; Horn et al., 2003). Annual age–length keys were developed based on these aged fish for each year and fishery.

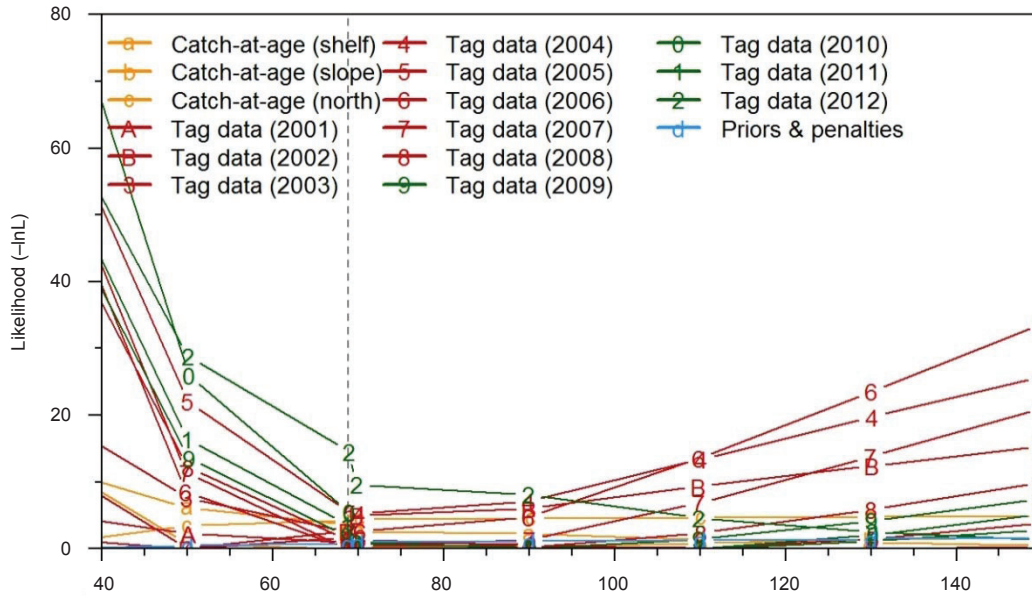The scaled length frequencies per year and fishery were multiplied by the annual age–length keys

Figure 2:   Likelihood profiles for B_0. Negative log likelihood values rescaled to have minimum 0 for each dataset. The dashed vertical line indicates the MPD.

for each year and fishery in order to obtain scaled age frequencies of the catches calculated for each year between 1999 and 2012 for Antarctic toothfish on the shelf, slope and north areas of the RSR (Hanchet et al., 2013; Parker et al., 2013a). The annual scaled age frequencies by fishery were used as observations to be fitted to the stock assessment model, as detailed in Appendix B.

Releases and recoveries of tagged fish

Releases and recoveries of tagged toothfish in the RSR were described in detail by Parker et al. (2013a). A mark-recapture program for Antarctic toothfish has been carried out in the RSR since 2001, and has been an ongoing requirement from CCAMLR to all vessels fishing in the Convention Area since 2004. A total of 32 755 Antarctic toothfish were released with tags by all vessels between 2001 and 2013, and 1 471 tagged fish were recaptured by 2013. Between 2 000 and 3 800 toothfish have been tagged and released in the RSR each year since 2004.

The numbers at length of toothfish tagged each year in each of the slope, shelf and north fisheries of the RSR were used as inputs to the stock assessment model. The numbers at length of toothfish recaptured each year for each release year from all fisheries combined were used as observations to which the model was fitted, as detailed below. Only

data of fish tagged and recaptured within the 'quality' data selection criteria were used in the stock assessment model.

Results

MPD results

The estimated initial biomass (B_0) for the model was 68 820 tonnes, whilst current biomass (B_{2013}) was 51 530 tonnes (75% of B_0). As described above, initial maximum of the posterior density (MPD) estimates were used to evaluate process error terms and model fits and to determine starting values for the three sets of Monte-Carlo Markov Chain (MCMC) posterior samples.

Likelihood profiles were carried out by fixing B_0 over a range of plausible values (40 000–150 000 tonnes), with the remaining parameters (e.g. selectivity functions) estimated. The components of the objective function were decomposed into the likelihood components from the observations (catch at age for each fishery and tag data each year) and the priors and penalties (Figure 2). The catch-at-age data and recaptures of tagged fish from 2005, 2009, 2010, 2011 and particularly 2012 suggested that very low biomass levels were less likely, whilst recaptures of tagged fish from 2002, 2004, 2006 and 2007 suggested that very high biomass estimates were less likely. The profiles were
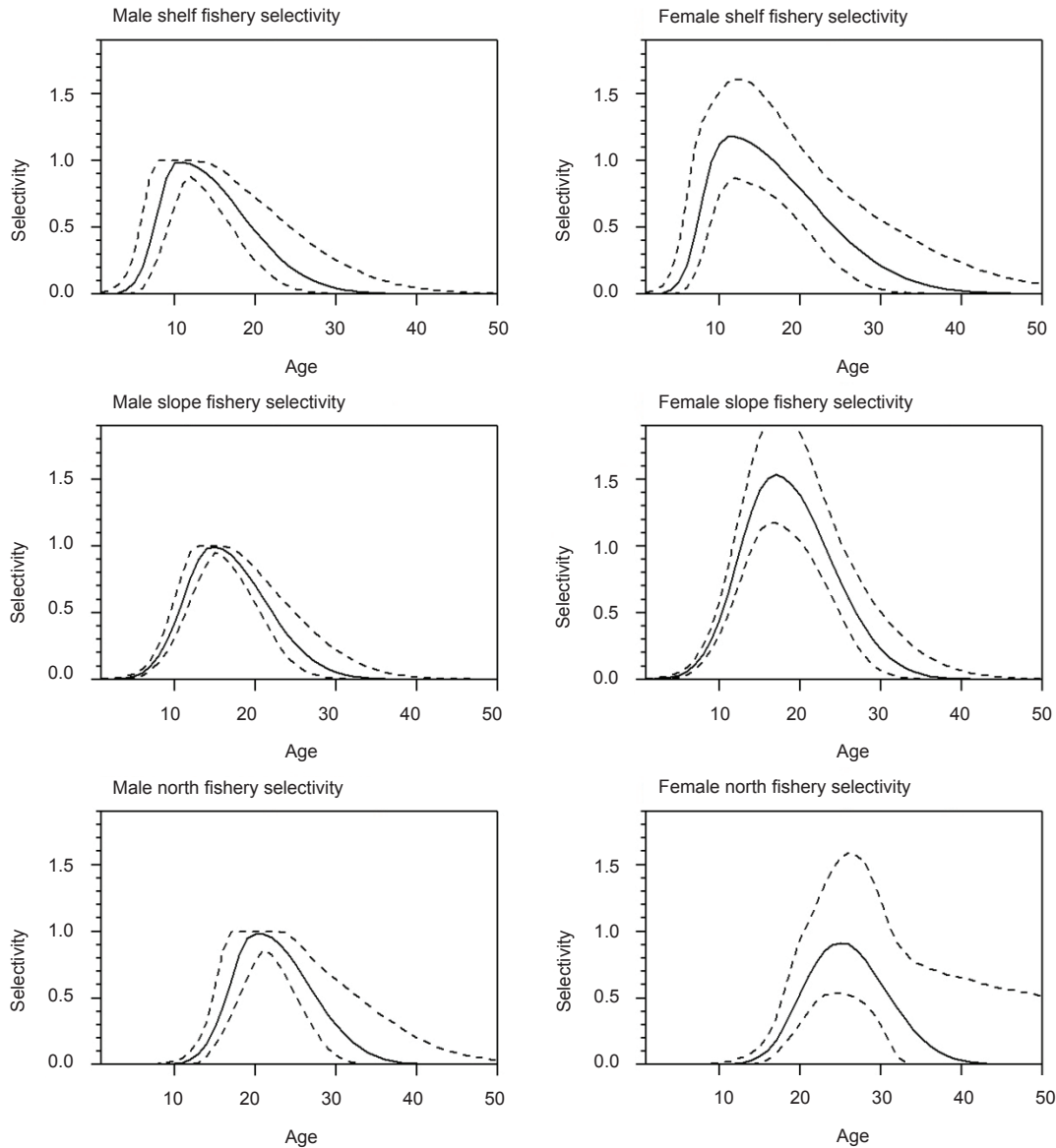
Figure 3: Estimated male and female selectivity ogives for the shelf, slope and north fisheries (solid lines indicate the median and dashed lines indicate the marginal 95% credible intervals).

influenced by the shelf catch-at-age proportions, suggesting that very low estimates of initial biomass were less likely.

Plots of the observed proportions at age of the catch versus MPD-expected values suggested that there was little evidence of inadequate model fit, but there appeared to be some evidence of non-random patterns in the residuals.

MCMC results

Trace plots showed no evidence of poor convergence in the key biomass parameters. Between-sample autocorrelations were also low, but there was some evidence of non-convergence

in the right-hand declining limb of both the male and female selectivity curves in the shelf fishery (Figure 3). The convergence test of Geweke (1992) and the Heidelberger and Welch (1983) stationarity and half-width tests also suggested some evidence of failure to converge in the right-hand limb parameters of some fishing selectivity curves. However, MCMC sensitivity analyses (where these parameters were fixed at MPD values) suggested that the lack of convergence in these parameters had little impact on the marginal posterior distributions of the key biomass parameters.

Estimates of the initial biomass and current biomass as a percentage of initial biomass are given in Figure 4. MCMC estimates of initial (equilibrium)
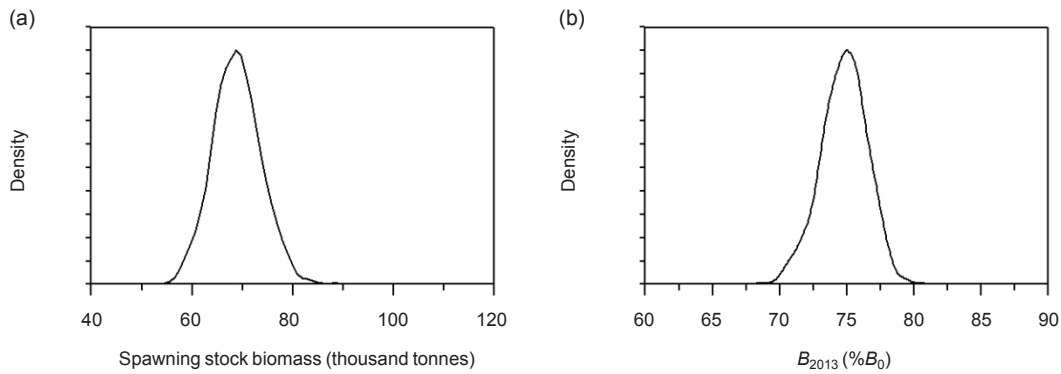
Figure 4: Posterior distribution estimates for (a) B_0 in thousands of tonnes, and (b) B_{2013} as a percent of B_0.

spawning stock abundance (B_0) were 68 790 tonnes (95% credible intervals 59 540–78 470); current (B_{2013}) biomass was estimated as 74.8% B_0 (95% CIs 71–78).

Estimated posterior densities of the observed and expected number of recaptured tagged fish at length, by release event and recapture year, are given in Figure 5. The mark-recapture data were moderately well fitted by the model in more recent years, although, in general, the number of recaptured fish at each length class was underestimated in earlier years. The fits to earlier mark-recapture data were poorer than those from more recent years, as in earlier years smaller fish were tagged preferentially, but since 2010 fish have to be randomly tagged and represent the length frequency of the fish caught. This disparity in earlier years accounts for the lower than expected number of tagged fish recaptured in those years.

The diagnostic plots of the observed proportions at age of the catch versus expected values did not indicate any strong evidence of inadequate model fit. Estimated selectivity curves appeared reasonable, with strong evidence of dome-shaped selectivity in all of the three fisheries (Figure 3).

Sensitivity analyses

A number of sensitivity analyses were carried out in order to better understand the potential implications of modelling decisions made on the results of the stock assessment and therefore management. If results are sensitive to specific decisions, then further care is needed in order to ensure these decisions are consistent with CCAMLR decision rules. The sensitivities detailed below are:

- a retrospective analysis investigated the impact of the four most recent years of data on the stability of the assessment, in particular, how sensitive the assessment might be to different areas being fished in different years

- the use of all tag data quantified the impact of the data selection on the model

- the use of a multinomial data-weighting method used previously in this stock assessment was investigated in order to quantify what impact different data-weighting methods might have on the assessment

- domed fishery selectivity functions allow for a cryptic biomass to be present in the model, which might impact on management decisions. The use of a logistic selectivity function in the north fishery was tested, as a proxy for assuming that no cryptic biomass was allowed in the model. It was only applied to the north fishery as this fishery represents the oldest adults of the population

- the use of sub-adult survey results was investigated in order to ascertain if a year-class strength (YCS) signal might be present in a survey, when it is not present in the fishery-dependent data.

A retrospective analysis was also run to investigate the impact of the most recent data on the stock assessment. First, the 2013 observations were excluded, then the 2012 and 2013 observations, then the 2011 to 2013 observations and finally the 2010 to 2013 observations were excluded. The retrospective models showed that the last three years of data suggest a higher biomass than previous data, with the most influential year, 2012, accounting for
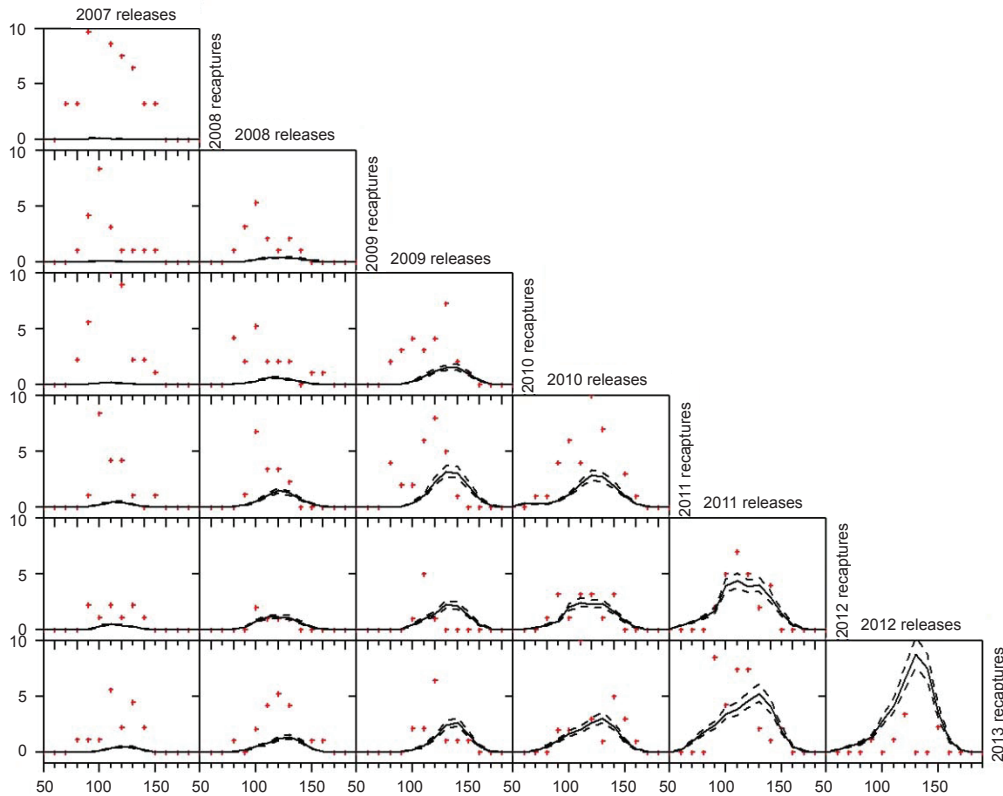
Figure 5:   Observed (points) and posterior estimates (lines, MCMC median and 95% credible intervals) of the number of tagged fish recaptured (y-axis) by length class (x-axis), year of release (columns) and year of recapture (rows).

a 7.5% increase in initial biomass, with all other years contributing to more modest increases in biomass.

The use of all mark-recapture data, rather than the selected dataset, resulted in an increase in initial biomass of over 20%. This result is unsurprising as the selection criterion resulted in 80% of tagged fish released being selected but only 72% of recaptures of tagged fish.

The use of multinomial data weighting, as previously used in this stock assessment, resulted in no change in the estimate of initial or current biomass, but in a reduction in the credible interval of the posterior distribution of the initial biomass from the MCMC, which was deemed too narrow. This narrowing of the credible interval is because the multinomial data-weighting method ignores autocorrelation between the age-frequency data within an age-frequency distribution, and therefore overestimates the weight of age data (see also Appendix A for further details).

In an alternative run, the northern selectivity function was assumed logistic in shape. This alternative hypothesis eliminates the potential for cryptic biomass which can be present under the assumption of a domed selectivity curve. Results suggested a slightly higher biomass (1% higher) under this assumption and associated slightly worse fits to the age data but no change in management advice.

The potential for estimating YCS was also investigated, either with or without inclusion of results from the sub-adult survey on the Ross Sea shelf autocorrelation (Parker et al., 2013b, 2013c). The sub-adult survey is designed as an annual time series but had only two years of data, so the runs were carried out as proof of concept. Without the sub-adult survey, the estimations of YCS were unstable, estimating a series of very low YCS with a very high YCS in the final year, regardless of the time period over which YCS were estimated. In contrast, when the results of the sub-adult survey were utilised in the model (both as an index of relative abundance and for age-frequency proportions),

the estimates of YCS were more stable, with values unchanged regardless of how many YCS were estimated.

Discussion

This paper outlines the development of a Bayesian sex- and age-structured population stock assessment model for Antarctic toothfish in the RSR. The modelling approach described incorporates a range of fishery-derived observations, including proportions at age, multiple tagging and recapture events, and other ancillary data. Model fits to the data were adequate, with the mark-recapture data providing the most information on stock size. MCMC diagnostics suggested some evidence of non-convergence, particularly in the declining right-hand limb of the fishing selectivity function parameters. However, multi-chain comparisons suggested that this would have little impact on the estimates of key model parameters and yield estimates.

In general, the mark-recapture data provided the most information on stock size, with the relative importance demonstrated by the likelihood profiles shown in Figure 2: they have the steepest curves with most pronounced minima and therefore hold the most information on the biomass. On the other hand, the profiles for age-frequency data tended to be flat, and therefore largely uninformative on the stock size. Observations from different years of release and recapture of tagged fish had differing impacts on the model estimates, with, for example, the recapture of fish tagged in 2012 most influential in increasing the estimate of initial and current biomass, while recaptures in 2006 contribute to an opposite effect. This is not unexpected because the locations of recaptures of tagged fish can be highly aggregated and most recaptured fish are seen to move only short distances. In 2006, for example, due to ice conditions, fishing was more concentrated in small-scale research units (SSRUs) 881H and M, areas where large numbers of tagged fish have been released over time and were available for recapture. On the other hand, in 2012, a large proportion of the fishing activity took place in SSRU 881K (Hanchet et al., 2013; Parker et al., 2013a) where there are fewer tagged fish available for recapture (Parker et al., 2013a). As a consequence, the number of tagged fish recaptured in 2006 was much higher than in previous years and that recaptured in 2012 was much lower than in previous years. This indicates that a key uncertainty underlying the

current model is the impact of movements and spatial structure in the Antarctic toothfish population, the potential effects of which are being evaluated in simulations using spatially explicit operating models (Mormede et al., 2014). Further, as components of the fleet either aggregate in previously fished locations or disperse to less fished locations (generally in response to ice conditions), the recapture rate of tagged fish is likely to fluctuate between years.

MCMC estimates of initial (equilibrium) spawning stock abundance (B_0) were 68 790 tonnes (95% credible intervals 59 540–78 470); current (B_{2013}) biomass was estimated as 74.8% B_0 (95% CIs 71–78). These estimates were used to set catch limits for the RSR toothfish fishery for the 2013 and 2014 fishing seasons (SC-CAMLR, 2013). Catch limits were estimated based on an assumption of constant future catch, where the stock biomass met the CCAMLR decision rules at a 35-year projection: less than 10% risk of dropping below 20% B_0 and expected average biomass at 50% B_0 at the end of the projection.

A number of sensitivity analyses were carried out. These showed that the use of the selected mark-recapture data, rather than all data, was a conservative assumption, that the data weighting chosen provided a wider and more likely credible interval than other methods, and that the stock assessment and its associated management advice were not dependent upon the hypothesis of cryptic biomass. Results also suggested that the sub-adult survey series which started in 2012 will provide a useful signal indicative of YCS as the time series develops, a signal which is not present in the fishery-dependent data.

Two other similar stock assessments of Patagonian toothfish in Antarctica have been published (Candy and Constable, 2008; Hillary et al., 2006). Both assessments have included CPUE data and, more importantly, fishery-independent survey data as well as mark-recapture and fisheries length-frequency data (yearly age-frequency data were not available at the time). Both came to similar conclusions, i.e. that CPUE data provided little information to the estimation of biomass, that the mark-recapture data was the most informative to the assessment and that the inclusion of age-frequency data would benefit the model. Both also concluded that estimating YCS was difficult, with

over-parameterisation of the model commonly observed along with seemingly spurious YCS estimates, despite fishery-independent surveys targeting juvenile toothfish. Therefore, the additional fishery-independent data to which these surveys had access did not provide much additional benefit compared with the data available for the stock assessment of Antarctic toothfish in the RSR.

This stock assessment of a CCAMLR exploratory fishery demonstrates the value of the multi-year tagging programs even with low recapture rates of tagged fish and in stocks where no fishery-independent estimates of adult biomass are available. The model described in this paper is sufficiently flexible to be used for a wide range of other species and fishing methods. It can include a number of years of tag-release and tag-recapture data, although the computer resources and time taken to run models can rapidly increase with more years of mark-recapture data. The approach is particularly useful for longer-lived species, where mortality due to tagging and tag loss are low, as under these conditions, the model maximises the use of mark-recapture data across multiple years. This is an important consideration where large-scale tagging programs are prohibitive due to their associated costs or due to difficulties in obtaining large numbers of fish.

Acknowledgments

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BIOLOGICAL PARAMETERS

Recruitment

For each stock, the number of fish added in year y is

$$R_y = R_0 \times YCS_{y-y\_enter} \times SR\left(SSB_{y-y\_enter}\right)$$ (A1)

where R_0 is the stock's average recruitment (ignoring the stock-recruitment function); YCS are year-class strength multipliers (also known as recruitment multipliers); y_enter is the number of years after it is spawned that a year class enters the partition; and SR is the stock-recruitment function.

Hanchet et al. (2013) and Paker et al. (2013a) found no strong evidence of YCS in the age frequency of Antarctic toothfish in the RSR. Therefore, YCS were not estimated in the model but instead set at 1 with future variability ($\sigma_R = 0.6$).

Recruitment was assumed to follow a Beverton-Holt relationship, whereby the stock recruitment (SR) is a function of the spawning stock biomass (SSB), the equilibrium is unfished spawning stock biomass (B_0) and is parameterised by the parameter *steepness*, defined as $h = SR(0.2B_0)$. The functional form for this relationship is:

$$SR(SSB) = \frac{SSB}{B_0}\Bigg/\left(1 - \frac{5h-1}{4h}\left(1 - \frac{SSB}{B_0}\right)\right).$$ (A2)

Recruitment was fixed, rather than being estimated, as suggested for example by He et al. (2006) and Kenchington (2014). Myers et al. (1999) estimated a steepness parameter (h) for a range of species using a meta-analysis approach; and Punt et al. (2005) analysed a wide range of stock and recruitment data to determine if these could lead to a choice of default values of priors for assessments of data-poor assessments, including h and σ_R.

Table 1 in Myers et al. (1999) summarises estimates of h. These values were used to derive plausible values of h. For species selected from the orders Gadiformes (including cods and hakes), Lophiiformes (monkfish), Ophidiiformes (lings), Scorpaeniformes (perch, rockfish) and *Anoplopoma fimbria* (sablefish), h was estimated at a median of 0.73, with an interquartile range of 0.46–0.83 and 90% percentile of 0.32–0.94.

Punt et al. (2005) analysed stock and recruitment data to estimate priors for the steepness of the stock-recruitment relationship. Their recommendations were based on the median posteriors of estimated values of steepness. They recommended that '… if a single default point estimate of steepness be used in a stock assessment, then the default should be $h = 0.907$ for Clupeiformes, Gadiformes, and Pleuronectiformes, and $h = 0.757$ for other species' (i.e. Aulopiformes, Perciformes, Salmoniformes and Scorpaeniformes).

Therefore, the spawning stock-recruitment relationship was assumed to be a Beverton-Holt relationship with steepness (h) equal to 0.75. CCAMLR management rules require that the stock be ultimately managed at 50% of initial biomass, a level at which the value of steepness has little impact on the stock-recruitment relationship. For example, a steepness of 0.7 would provide 90% of unfished recruitment at 50% biomass, and a steepness of 0.75 would provide 92%; even steepness as low as 0.46 would provide over 75% of unfished recruitment. Therefore, the current model and prospective use for management of this stock is unlikely to be sensitive to the choice of these parameters, as shown by Hillary et al. (2006) for Patagonian toothfish.

Table A1: Estimates of instantaneous natural mortality (M, in y^{-1}) for Ross Sea Antarctic toothfish, by sex for the north fishery area. For the Chapman-Robson method, $A_x = A_r$; for the Hoenig and Punt methods, $A_x = A_{1\%}$.

Sex	Method	North	
		A_x	M
Male	Chapman-Robson	16	0.15
	Hoenig	37	0.11
	Punt	37	0.14
Female	Chapman-Robson	19	0.17
	Hoenig	36	0.12
	Punt	36	0.14

Natural mortality

Natural mortality (M) was derived using three methods: Chapman and Robson (1960), Hoenig (1983) and Punt et al. (2005). Catch-at-age data between 1998 and 2005 in the north fishery only was used; shelf and slope fisheries data were not used as they are not expected to include the oldest fish (Hanchet et al., 2013; Parker et al., 2013a).

Estimated total numbers at age in the catch were summed across each age class between 1998 and 2005 to produce a single distribution for each sex. Where several years of data are combined in this way, it has the effect of smoothing the data and reducing the influence of any particularly weak or strong year classes. An estimate of instantaneous natural mortality (M) was derived using the Chapman-Robson equation

$$M = \log_e\left(\frac{1 + a - 1/n}{a}\right) \tag{A3}$$

the method of Hoening (1983),

$$\log_e M = 1.46 - 1.01 \times \log_e A_{1\%} \tag{A4}$$

and Punt et al. (2005)[1],

$$\log_e M = 0.97 - 0.822 \times \log_e A_{1\%} \tag{A5}$$

where $A_{1\%}$ is the minimum age of the oldest 1% of fish in the commercial catch. These estimates are also listed in Table A1.

There is no clear evidence that M for Antarctic toothfish differs between sexes, although males mature earlier than females.

The Chapman-Robson method technically estimates the total instantaneous mortality (Z) rather than natural mortality M. However, the Ross Sea fishery had been in progress for less than eight years by 2005 (the lowest A_r used in the calculations is 8) and total extractions had probably been low relative to total

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[1] The equations listed in Table 14 of Punt et al. (2005) appear incorrect, in that they describe the relationship as a function of $\log_{10}$ rather than (as described in Figure 11 of that report) $\log_e$. The relationships calculated here use $\log_e$.

biomass. The Chapman-Robson values can be used to infer a likely maximum value of M. Furthermore, a review by Kenchington (2014) of estimation methods for M suggests that estimates based on maximum age are the most reliable.

Estimates of M derived using the methods of Hoenig (1983) and Punt et al. (2005) ranged from 0.11 to 0.14 y^{-1}. For Patagonian toothfish, estimates of M were revised to 0.13 y^{-1} for Subarea 48.3 (Hillary et al., 2006) and 0.155 y^{-1} using mark-recapture data (Candy, 2011). A value of 0.13 y^{-1} was chosen for stock modelling of Antarctic toothfish for both males and females, being a value towards the lower end of the plausible range.

Maturation

A fixed logistic relationship of maturity at age was assumed, with estimable parameters a_{50} and a_{to95}. The logistic ogive takes values 0.5 at $x = a_{50}$ and 0.95 at $x = a_{50} + a_{to95}$:

$$f(x) = 1 \Big/ \Big[1 + 19^{(a_{50} - x)/a_{to95}} \Big].$$ (A6)

Over 1 100 gonad samples of toothfish from the RSR were histologically analysed in order to assess age at spawning, including skip-spawning (Parker and Grimes, 2010), and updated with additional data (Parker and Marriott, 2012). Using the estimates of Parker and Marriott (2012) and given in Table 1, the age at which 50% of fish spawn (a_{50}) was calculated at 16.9 years for female Antarctic toothfish in the RSR, and 12.0 years for males. Evidence of skip-spawning was seen in adolescent females only, and resulted in a flatter, right-shifted ogive for females. Values of a_{to95} were 7.7 years for females and 5.2 years for males.

Growth parameters

The von Bertalanffy growth equation (von Bertalanffy, 1938) was used to derive the mean length-at-age relationship, parameterised by L_{inf}, k and t_0 to derive the mean length at age ($\bar{s}$)

$$\bar{s}(age) = L_{inf}\left(1 - \exp\left(-k\left(age - t_0\right)\right)\right).$$ (A7)

Over 4 500 Antarctic toothfish from the RSR were aged between 1998 and 2005, using validated aging methods (Horn, 2002; Horn et al., 2003; Sutton et al., 2012). These data were used to estimate the von Bertalanffy parameters using maximum likelihood, where growth curves were fitted assuming normally distributed errors with a standard deviation that increased as a function of mean length at age rather than as a function of age. Here, the length-at-age data for each sex separately was assumed to consist of length L and age t, observations for n fish are partitioned into groups. Then the likelihood function of the parameters θ_i for the ith group, assuming normally distributed errors parameterised with a constant coefficient of variation c (estimated) that is assumed to be the same for all groups, is described as LH:

$$LH_i\left(\theta_i, c; L_i, t_i\right) = \prod_{j=1}^{n_i} \left(2\pi\left[c\mu\left(\theta_i, t_{ij}\right)\right]^2\right)^{-\frac{1}{2}} \times \exp\left(-\frac{1}{2\left[c\mu\left(\theta_i, t_{ij}\right)\right]^2}\left[L_{ij} - \mu\left(\theta_i, t_{ij}\right)\right]^2\right).$$ (A8)

Calculated von Bertalanffy growth parameters are listed in Table 1 and the curves and raw data are plotted in Figure A1. Von Bertalanffy parameters were not calculated for the three areas separately because there are very few small fish caught in the northern area, and very large fish are uncommon on the shelf, therefore it is likely that any growth curves calculated for these areas would not be representative of the entire population.
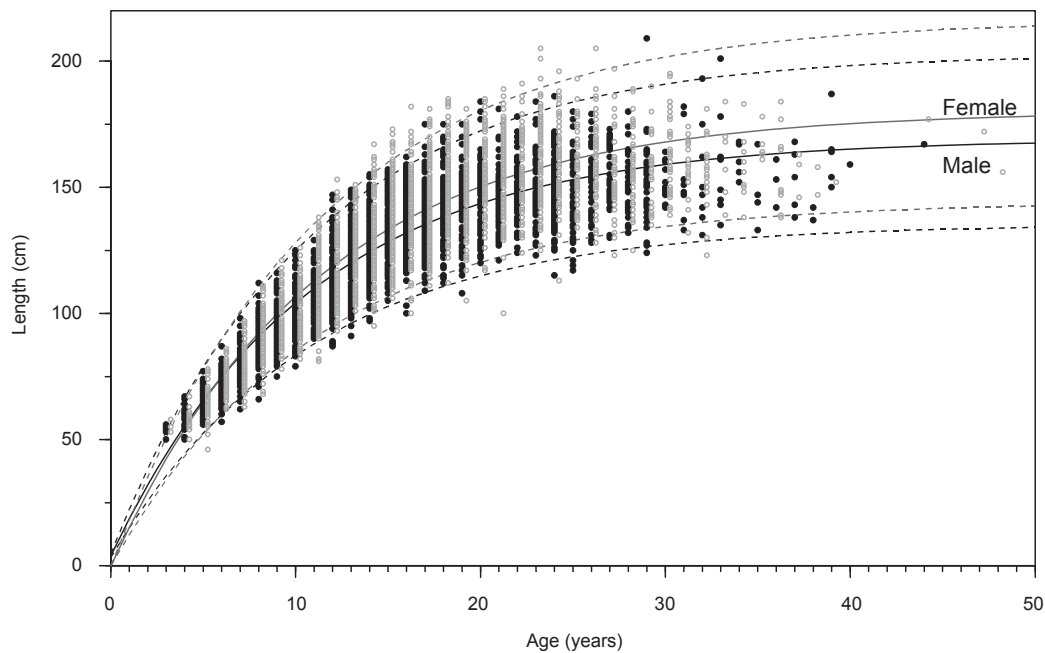
Figure A1:   Von Bertalanffy growth curves for males (black lines) and females (grey lines) for Antarctic toothfish in the Ross Sea, with points showing the observations of age at length for males (filled circles) and females (open grey circles). Dashed lines show 95% confidence intervals.

Length–weight relationship

The length–weight relationships for Antarctic toothfish by sex, with parameters *a* and *b*, was given by:

mean weight = $a \times$ (mean size at age)^b.

The dataset comprised over 130 000 length–weight records from all longline vessels fishing in the Ross Sea up to the end of 2005. The length–weight parameters are listed in Table 1, and the curves and raw data are plotted in Figure A2. Variability in the length–weight and length-at-age relationships were assumed and parameterised by a normal distribution, with constant CV = 0.1.

Tagging parameters

The modelling framework used allowed for the specification of a number of tag-related parameters: tag-detection rate, tag-loss rate and initial tag mortality. These parameters were fixed based on external analyses of the Ross Sea fishery mark-recapture data or information available in the literature. Details of the mark-recapture program in the RSR and rationale for some of the parameter values are detailed in Parker et al. (2013a).

Each fishing vessel operating in the RSR is required to carry two scientific observers. Part of their duty is to observe about 40% of every line hauled. Moreover, being a longline fishery, each fish is handled individually when hauled. Therefore, the actual tag-detection rate is assumed at 100%. However, as 1.4% of recaptures of tagged toothfish in the RSR could not be linked to a release event (Parker et al., 2013a), the tag-detection rate used in the model is 98.6% to account for these unlinked tagged fish. In comparison, tag-detection rates of 99.3% were calculated for the Patagonian toothfish longline fishery in Heard and McDonald Island and between 94% and 99% for their trawl fisheries (Candy and Constable, 2008).

Antarctic toothfish in the RSR have been tagged since 2001 and routinely double-tagged since 2004. By 2010, a total of 64 toothfish which had been double-tagged were recaptured with a single tag, allowing the calculation of initial and ongoing tag-loss rates for toothfish in the RSR (Parker et al., 2013a). Initial tag
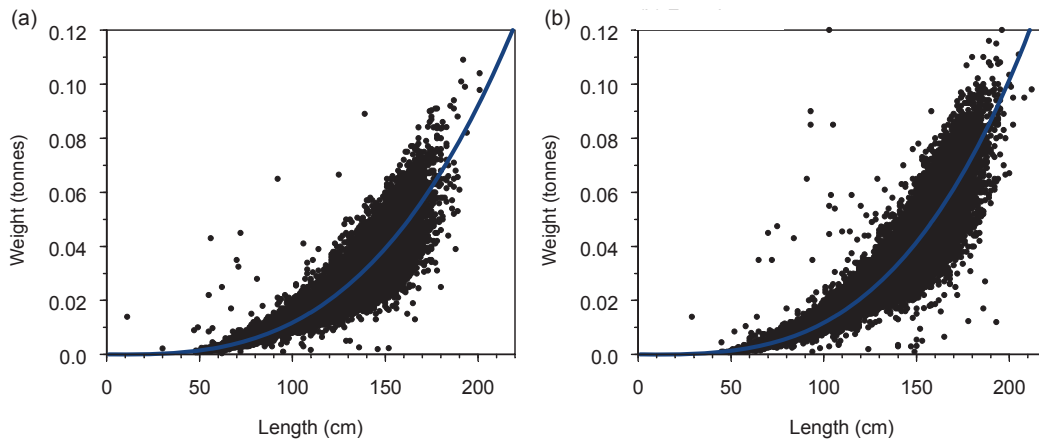
Figure A2: Length–weight curves (grey lines), by sex, for Ross Sea Antarctic toothfish, with points showing the observations of weight at length.

loss of 3.3% per tag and the individual instantaneous tag-loss rate of 0.062 y^{-1} per tag were calculated and used in the model. Tag-loss rates in each individual year were calculated taking into account the percentage of double-tagged fish released in that year.

Based on an at-sea experiment, Agnew et al. (2006) estimated the initial mortality of Patagonian toothfish in Subarea 48.3 from tagging as 10% when considering all toothfish, and 5% when considering only toothfish in good condition. Moreover, Agnew and Belchier (2009) estimated length-specific mortality in Patagonian toothfish. In the absence of any further information available for Antarctic toothfish, an initial tag-related mortality at release of 10% was assumed in the model for all tagged toothfish regardless of their length at tagging, even though observers are required to only tag toothfish in good condition. No further ongoing tag-related mortality was applied to tagged fish, as there is no current evidence for such ongoing mortality (natural mortality was applied as for any fish in the model).

Based on length data of Antarctic toothfish tagged and subsequently recaptured, tagging was also assumed to result in a retardation of growth in individual fish. Parker et al. (2013a) estimated that this effect was the equivalent to a period of zero growth immediately following tagging of approximately 0.5 year, followed with normal growth. Hence, the t_0 von Bertalanffy growth parameter for tagged fish inside the model was adjusted by –0.5 year, i.e. the effective size at age for a tagged fish was assumed to be the size of a fish aged 0.5 years less than that of an untagged fish, but that growth was otherwise at the same rate as untagged fish.

MODEL DETAILS

Model structure

The stock assessment model was structured with ages from 1–50, whereby the number of male and female toothfish of each age from 1 to 50 was tracked through time, and the last age group was a plus group (i.e. an aggregate of all fish aged 50 and older). The population was initialised assuming an equilibrium age structure at an unfished equilibrium biomass, i.e. with constant recruitment. The initial biomass was estimated by the model. The model was run from 1995 to 2013, and the annual cycle was broken into three discrete time steps, nominally summer (November–April), winter (May–October) and an age-incrementation step.

Recruitment was assumed to occur at the beginning of the first (summer) time step, to be 50:50 male to female and to be the mean (unfished) recruitment (R_0) multiplied by the spawning stock-recruitment relationship.

The population model structure included multiple annual tag-release events in order to model the mark-recapture data. Here, the model structure as described above was replicated for each annual set of releases of tagged fish, with the numbers at age and sex in the tag component defined by the annual tag-release identifier. Each tagging event was defined as the end of the first time step. Numbers of fish in the tagged component were then modified by initial tag-related mortality (as a proportion) and then subsequent ongoing annual tag loss (at a constant rate). The population processes (natural mortality, fishing mortality, ageing, etc.) were then applied collectively over the tagged and untagged components of the model. The numbers at age of recaptured fish with a tag are also removed from the appropriate tagged component of the population. As tag-release data were only available as numbers at length (not age or sex), the proportions of tagged fish at age and sex were determined within the model by multiplying the observed proportions of fish tagged at length by the proportions of fish at age/sex by length assumed by the model for the overall population. The numbers of tagged fish at length recaptured each year for each tag-release event were provided to the model as observations to be fitted to.

As the fishery operated only during the summer months (typically December–March), fishing mortality was applied only in the first (summer) time step. Fishing mortality was applied by removing half of the natural mortality for the time step (a quarter of the total annual mortality), the mortality from the fisheries instantaneously, then the remaining half of the natural mortality for the time step. Fishing mortality was applied for the three fisheries separately (shelf, slope and north), using different selectivity functions for each of these fisheries to reflect the different age distributions of fish in the catch in the three fisheries. The selectivity parameters were estimated by the model through fitting of the observations, particularly the fisheries age-frequency data.

The maturation process was applied in the second time step (winter), as Antarctic toothfish are thought to mature and spawn in winter (Hanchet et al., 2008). Maturation was specified as the time-invariant proportion of male and female fish at age that were mature. In the second time step, the remaining half of annual natural mortality was also applied.

In the final time step, all fish aged by one year, with fish in the 50-plus group remaining in that group. Biomass calculations at any point in the model were made by multiplying the number of fish in each year class by the size-at-age relationship and the length–weight relationship for each sex separately.

Modelling framework

The model was carried out using the generic software package CASAL, which is a robust, documented and validated, yet flexible, software tool for stock assessments (Bull et al., 2012). It allows easy documentation and peer review of individual models with greater transparency and quality assurance procedures without compromising the flexibility which might be required when assessing varied stocks. It has been used in CCAMLR for a number of years for Patagonian toothfish stock assessments (e.g. Candy and Constable, 2008; Hillary and Agnew, 2006).

Fishery selectivity functions

A total of 35 parameters were estimated within the model: B_0, the three fishery selectivity ogives by sex ($n = 21$), annual shift coefficient for the north and slope fisheries ($n = 1$ each) and an annual shift parameter for the shelf fishery ($n = 12$). These are detailed below.

For each parameter, priors were chosen that were relatively non-informative but were also, given the precautionary CCAMLR management approach, likely to encourage lower, rather than higher, estimates of initial and current biomass. The prior for initial biomass (B_0) was uniform-log (Hillary et al., 2006), while priors for all other parameters were uniform.

For each of the three fisheries, a selectivity coefficient for males at age was defined to have a range of 0–1, and female selectivity coefficient a range of $0–a_{max}$ using double-normal ogives. Each double-normal ogive was parameterised using four estimable parameters: a_1 (the mode), s_L (increasing left-hand limb shape parameter), s_R (decreasing right-hand limb shape parameter) and a_{max} (value at a_1 for males, with value of 1 for females), where the value at age x was defined as

$$f(x) = a_{\max} \times 2^{-[(x-a_1)/s_L]^2}, \qquad (x \leq a_1)$$
$$= a_{\max} \times 2^{-[(x-a_1)/s_R]^2}, \qquad (x > a_1). \qquad \text{(B1)}$$

There is a positive correlation between toothfish length and depth (Hanchet et al., 2003) and because of varying fleet, ice conditions and management restrictions, the depth fished has varied between years. To account for this, annual shifts in the selectivity functions were also estimated for the slope and north fisheries, which allowed the selectivity function to 'shift' to the left or right with changes in the mean depth fished. The shift in annual selectivity functions was parameterised by $a_1 = a(E_y - \bar{E})$, where a was the shift coefficient (y.km^{-1}) and E_y was the mean depth fished (km, weighted by the catch) of all sets in the fishery in year y, and $\bar{E}$ was the mean of the E_y's.

However, on the shelf, the relationship between median toothfish length and depth was less clear, as fishing did not occur consistently across the regions over years. Hence, for the shelf fishery, shifts in annual selectivity functions were estimated as independent parameters. Following advice from CCAMLR's Working Group on Fish Stock Assessment, a sensitivity run removing these parameters showed that they had no impact on the biomass estimate of the stock assessment, even though fits to the age data were slightly worse.

Model estimation

Fitting catch-at-age observations

The catch proportions-at-age data were fitted to the modelled proportions-at-age composition using a multinomial likelihood, where O is the observations for a single year in a proportions time series, expressed as a vector of n proportions summing to 1; E is the corresponding fitted values; N the 'effective sample size' parameter; and Z a robustifying function to avoid division by zero errors.

Table B1: Numbers of Antarctic toothfish with tags released for the years 2001–2013, and the number recaptured in 2002–2013 (ignoring within-season recaptures) for selected trips (from Parker et al., 2013a). Numbers in italics correspond to fish which have been at liberty for more than six years.

Released fish		Recaptures												
Season	Number	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012	2013	Total
2001	259	1	1	0	0	0	1	*1*	*1*	*0*	*0*	*0*	*0*	5
2002	684	2	9	3	9	8	13	6	5	*2*	*3*	*0*	*1*	61
2003	834	-	6	9	9	2	8	2	2	*1*	*2*	*2*	*0*	43
2004	1 221	-	-	4	19	17	26	22	5	10	*10*	*6*	*12*	131
2005	2 691	-	-	-	6	21	27	27	7	34	10	*11*	*11*	154
2006	2 257	-	-	-	-	11	87	67	13	20	13	0	*6*	217
2007	2 921	-	-	-	-	-	18	58	21	46	20	10	19	192
2008	2 151	-	-	-	-	-	-	13	16	20	17	5	20	91
2009	1 825	-	-	-	-	-	-	-	5	27	28	7	14	81
2010	2 170	-	-	-	-	-	-	-	-	21	49	16	27	113
2011	2 213	-	-	-	-	-	-	-	-	-	7	25	31	63
2012	2 115	-	-	-	-	-	-	-	-	-	-	7	8	15
2013	2 285	-	-	-	-	-	-	-	-	-	-	-	9	9
Total	23 626	3	16	16	43	59	180	196	75	181	159	89	158	1 175

$$-\log(L) = -\log(N!) + \sum_i \left[\log\big((NO_i)!\big) - NO_i \log\big(Z(E_i, r)\big) \right].$$ (B2)

Ageing error was assumed and modelled by modifying the likelihood for the proportions-at-age data such that E_i was replaced by E'_i, where E'_i is the expected proportion at age multiplied by an ageing error misclassification matrix. The misclassification matrix was derived by assuming that the ageing error was unbiased and normally distributed with constant coefficient of variation (CV) of 0.1.

Fitting mark-recapture observations

The numbers of tagged fish released and recaptured by year for the selected trips used in the model are summarised in Table B1. Within-season recaptures were ignored (i.e. not included in the tag-release numbers) and hence recapture observations were defined for each release event in each subsequent year. The estimated number of scanned fish (i.e. those fish that were caught and inspected for a possible tag) was derived from the sum of the scaled length frequencies from the scientific observer records (i.e. the size distribution of the landed catch given by Hanchet et al., 2014) plus the numbers of fish tagged and released. Recapture events of tagged fish were all assumed to occur at the end of the first (summer) time step.

For each year, the numbers at length of tagged fish recovered for each release event t were fitted, in 10 cm length classes (range 40–220 cm), using a binomial likelihood, i.e.:

$$-\log(L) = \sum_i \left[\log(n_i!) - \log\big((n_i - m_i)!\big) - \log(m_i!) + m_i \log\left(\frac{M_i}{N_i}\right) + (n_i - m_i)\log\left(1 - \frac{M_i}{N_i}\right) \right]$$ (B3)

where n_i = number of fish in length class i that were scanned, m_i = number of tagged fish in length class i that were recaptured from the release event t, N_i = expected number of fish in length class i in the population and M_i = expected number of fish in length class i in the tagged population from t.

Sample size estimates and data weighting

Estimates of the effective sample size for the proportions-at-age observations were derived by assuming that the relationship between the observed proportions, O_{ij}, and estimated CVs, c_{ij}, followed that for a multinomial distribution with unknown sample size N_j, for age class i in year j. The estimated sample size was then derived using a least squares fit of $\log(c_{ij}) \sim \log(O_{ij}) - \tfrac{1}{2}\log(N_j)$.

Additional variance (termed process error), assumed to arise from differences between model simplifications and real-world variation, was added to the sampling variance for all observations. Adding such additional errors to each observation type has two main effects: (i) it alters the relative weighting of each of the datasets (observations) used in the model, and (ii) it typically increases the overall uncertainty of the model, leading to wider credible bounds on the estimated parameters. The additional variance was estimated following the methods by Francis (2011a, 2011b).

Age- or length-frequency data are internally correlated: positively correlated with nearby bins and negatively correlated otherwise. This property leads to overweighting of data when using multinomial and other weighting methods. In the methods by Francis (2011a, 2011b), the weights are calculated so as to be consistent with the errors in mean age, which avoids autocorrelation issues inherent to other methods.

The weight w_j to be applied to each age-frequency distribution is calculated as follows:

$$w_j = 1 \bigg/ \mathrm{var}_i\!\left[\left(O_{ij} - E_{ij}\right)\!\bigg/\!\left(v_{ij}/N_{ij}\right)^{0.5}\right] \tag{B4}$$

where N_{ij} was the number of multinomial cells, O_{ij} is the observed proportions for age class i in year j, E_{ij} is the expected proportions and v_{ij} is the variance of the expected age distribution.

For each fishery, the weight is then applied to the sample size calculated in the previous step, before re-running the model at maximum of the posterior density (MPD) level.

Finally, the over-dispersion for the tag-recapture likelihoods is estimated using a similar method to that for the proportions-at-age data. First, initial sample sizes for the numbers recaptured and the numbers scanned are assumed from the actual numbers recaptured and numbers scanned and, second, the over-dispersion ϕ_j for each tagging event is calculated from its i recapture events, from an initial MPD run, where

$$\phi_j = \mathrm{var}\!\left(\frac{O_{ij} - E_{ij}}{\sqrt{E_{ij}}}\right) \tag{B5}$$

where O_{ij} was the observed number of recaptures and E_{ij} the expected number of recaptures. The log-likelihood is then modified by multiplying by $1/\phi$.

The weight for age frequencies was estimated between 0.004 and 0.14 for the different data sources and $\phi = 5.6$.

Minimisation

Model parameters were estimated by minimising the total objective function, which was the sum of the negative log-likelihoods from the data, the negative-log priors and the penalty functions used to apply model constraints. Penalties were applied to both catch and mark-recapture data.

Initial fits were evaluated at the MPD, and data weightings determined by considering MPD fits and residual patterns and qualitative evaluation of MPD profile distributions (i.e. by evaluating the minimum objective function while fixing one parameter and allowing all other parameters to vary).

The joint posterior distribution of the model parameters were then estimated using a Bayesian approach, using Monte Carlo Markov Chain (MCMC) estimates from an implementation of the Metropolis algorithm (Gelman et al., 1995; Gilks et al., 1998). Chains were initialised using a random starting point near the MPD (generated from a multivariate normal distribution, centred on the MPD, with covariance equal to the inverse Hessian matrix), with correlation matrix derived from the inverse Hessian.

MCMCs were estimated using a burn-in length of 4×10^5 iterations, with every 1 000th sample taken from the next 1×10^6 iterations (i.e. a sample of length 1 000 was taken to estimate the Bayesian posterior distribution). Chains were investigated for evidence of non-convergence using multiple-chain comparisons, standard diagnostic plots, chain autocorrelation estimates and single-chain convergence tests of Geweke (1992) and the stationarity and half-width tests of Heidelberger and Welch (1983).